Evaluating ecohydrological modeling framework to link atmospheric CO_2 and stomatal conductance

Short title: Evaluation of stomatal conductance models

Xuefei Lu and Lixin Wang*

Department of Earth Sciences, Indiana University-Purdue University Indianapolis (IUPUI), Indianapolis, IN 46202, USA

* Correspondence to: Lixin Wang (lxwang@iupui.edu)

Lixin Wang
Department of Earth Sciences
Indiana University-Purdue University Indianapolis
Indianapolis, IN 46202, USA
Office phone number: 1-317-274-7764
Fax: 1-317-274-7966

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Abstract

The establishment of an accurate stomatal conductance (g_s) model in responding to CO_2 enrichment under diverse environmental conditions remains an important issue as g_s is the key to understand the plant-water-atmosphere interactions. A better representation of g_s is important to reduce uncertainties in predicting the climate change impacts on various ecosystem functions. In this study, we evaluated three most commonly-used g_s formulations for the estimation of the stomatal response to environmental factors using *in situ* measurements under different environmental conditions. The three g_s models were Leuning's modified Ball-Berry model, and two specific cases of the optimization models (i.e., Rubisco limitation model and RuBP regeneration limitation model). Based on an analysis of 234 data points obtained from experiments under instantaneous, semi-controlled and the Free-Air CO_2 Experiment (FACE) conditions, we found that Leuning's modified Ball-Berry model and RuBP limited optimization model showed similar performance and both performed better than Rubisco limitation model. Functional groups (e.g., C_3 versus C_4 species) and life form (e.g., annual versus perennial species) play an important role in determining the g_s model performance and thus pose a challenge for g_s predictions in mixed vegetation communities.

Keywords: ecohydrology, empirical model, economic model, optimization model, mechanistic model, stomatal conductance

1 Introduction

Stomata control the water losses and CO_2 uptake between plant and atmosphere, and therefore play a key role in determining the vegetation response to climate change. Stomatal conductance (here after g_s) modeling has long been used as an effective and well-adapted tool to study the physiological controlling mechanisms of stomata. A large number of studies have modeled the stomatal behavior as the function of environmental factors, such as CO_2, light, relative humidity or vapor pressure deficit (Jarvis 1976, Cowan and Farquhar 1977a, Ball et al. 1987, Leuning 1995). However, stomata respond to environmental stimuli in a complex way so it has been challenging to design a g_s model that is capable of dealing simultaneously with all the environmental factors. The establishment of a reliable and general stomatal conductance model remains an important research problem since g_s is the key to understand the plant-water-atmosphere interactions and how changing climate affects the three-way interactions.

A better representation of g_s is important to reduce uncertainties in predicting the climate change impacts on various ecosystem functions. Climate change is causing more frequent and extreme summer heat waves (IPCC 2012), a phenomena that have major environmental, social and economic consequences (IPCC 2012). A recent study shows that different g_s models can have a profound effect on the simulation of heat-weaves under future climates (Kala et al. 2016). Robust models of stomatal conductance, therefore, have been crucial in advancing our understanding how climate change affects frequency and intensity of heat waves. Studies also show that model projections of climate change impacts on terrestrial ecosystems could have large uncertainty because most global vegetation models have down-regulated the photosynthesis or stomatal conductance using simplistic soil water limitation function (Trugman et al. 2018). Better representations of stomatal conductance response to water stress are greatly needed to improve the projections of global land carbon sink. A

recent advance in the study of stomata used the carbon-maximization hypothesis to predict functional response of stomata to changes in CO_2 and vapor pressure deficit, which accounts for plant competition for water and directly incorporates the effects of soil and leaf water potential (Wolf et al. 2016).

There are three basic approaches to model stomatal conductance: namely empirical approach, mechanistic (process-based) approach, and economic (optimization-based) approach (Buckley and Mott 2013). Most leaf and canopy gas exchange studies use the empirical (phenomenological) models because they are simpler and in many conditions they agree with the direct g_s measurements (Buckley and Mott 2013). The widely used empirical models include the multiplicative and empirical model of Jarvis (1976), 'Ball-Berry' model (1987), and modified 'Ball-Berry' model by Leuning (1995). The major limitation of such models is that the empirical approach relies on the choice of certain sets of empirical parameters and the use of statistical correlations to assume a link between the mechanism and the process (Adams et al. 2013). So the empirical models do not fully describe the system behaviors and interactions. It is worth noting, however, both Ball-Berry' model and Leuning's modified 'Ball-Berry' model have showed good agreement with observations across a broad range of vegetation types (Ball et al. 1987, Collatz et al. 1992, Harley et al. 1992, Leuning 1995).

To address the limitations of empirical models, some recent studies have attempted to model g_s in a more mechanistically explicit way (e.g., Dewar 2002, Gao et al. 2002). The mechanistic models focus on simulating detailed physical or biological processes that explicitly describe the mechanisms of stomatal control, thereby are more comprehensive and incorporate mechanisms explicitly (Adams et al. 2013, Buckley and Mott 2013). Yet the mechanistic knowledge is often difficult to translate into mathematic framework (Damour et al. 2010), and their parameters for biophysical properties are difficult to measure by

experiments (Buckley and Mott 2013). In reality, the mechanistic models are less often used to predict the environmental stimuli's impact on g_s in the cellular and subcellular processes. It is generally easier to build models using empirical observations, so the majority of stomatal conductance models are 'semi-empirical", which means that the models are built on physiological mechanisms, but are combined with empirical functions (Damour et al. 2010).

The optimization approach is pioneered by Cowan & Farquhar (1977b), based on the theory that plants tend to maximize CO_2 assimilation for a fixed amount of water loss or tend to minimize water loss for a fixed amount of CO_2 assimilation. The optimal stomatal theory was mathematically expressed as the marginal water cost per unit carbon gain $\partial E/\partial A_{net}$ (i.e., the ratio of the sensitivities of rate of transpiration (E) and net carbon assimilation (A_{net}) to changes in g_s), assuming that the ratio remains constant and equals to the Lagrange multiplier λ during a finite time interval (i.e., within a given day) (Cowan and Farquhar 1977a, Damour et al. 2010). Although there has been debate that λ may vary with environmental conditions and difficult to measure (Collatz et al. 1992, Makela et al. 1996, Buckley 2007), the optimization models have recently received renewed interest because they do not require a priori specification to describe the response of stomatal conductance to environmental variables (Manzoni et al. 2011, Medlyn et al. 2011). The optimization models provide a close-form expression for g_s as a function of environmental variables and an additional parameter λ (Vico et al. 2013). There are two major assumptions for optimization models, in which Katul (2009) and Lloyd and Farquhar (1994) assumed that stomata were optimized for Rubisco-limited conditions (i.e., under saturating light or at low CO_2 concentration within the sub-stomatal cavity), while Medlyn et al. (2011) focused on conditions where photosynthesis was limited by RuBP regeneration (i.e., under limited light or at high atmospheric CO_2 concentration).

Studies of stomatal response to environmental conditions using different methods generally have good performance in non-water stressed conditions, but not in water-stressed conditions like drylands. Soil moisture is a limiting factor in dryland vegetation growth and function (Rodriguez-Iturbe and Porporato 2004, Wang et al. 2012), however, most stomatal conductance models seemingly under-predict the soil moisture effect on stomatal conductance, due to its simplicity in representation of the soil moisture function in these models.

In this study, we aim to evaluate three most commonly-used and relatively simple g_s models for their estimation of the stomatal response to environmental stimuli. Previous studies have typically tested g_s models on specific conditions, while in this study, we attempt to evaluate the different g_s models under different environmental conditions, using *in-situ* data from three types of measurements: (1) the instantaneous measurement of g_s, (2) the measurement of g_s from semi-controlled plant growth facility, and (3) g_s responses in the Free-Air CO_2 Experiment (FACE). We also test how well the predictability of different models is against dryland data.

2 Methods

2.1 Model Formulation

In this study, we tested three g_s models: the Leuning's modified Ball-Berry model that is the modification of a widely used semi-empirical Ball-Berry approach, and the two simple solutions to the stomatal optimization theory for estimating g_s: the optimization model for RuBP regeneration limitation, and the optimization model for Rubisco limitation. These two cases presented the optimal conditions and they assumed that stomata aperture was optimized either under RuBP regeneration limitation or under Rubisco limitation only. Although the mechanistic models are theoretically better for predicting the stomatal response to

environmental stimuli, the complex parameterizations make it difficult to parameterize under the field setting (thus challenging to evaluate using the field data), and therefore no mechanistic model was chosen for this study.

1. Ball-Berry and Leuning's stomatal conductance models

Ball et al. (1987) developed one of the most commonly used models of g_s. In Ball's model, it assumes that stomatal conductance is a function of photosynthetic rate (A), CO_2 concentration at the leaf surface (C_a), and humidity deficit (D). Leuning (1995) has suggested a hyperbolic function of D for humidity response, so the mathematical form of Leuning's modified Ball-Berry model is given by

$$g_s = g_0 + a_1 \frac{A}{(C_a - \Gamma)(1 + D/D_0)}, \quad (1)$$

where g_0, a_1 and D_0 are empirically determined coefficients, and Γ is the CO_2 compensation point, which is zero for C_4 plant (Cox et al. 1998).

Cox et al. (1998) showed that both Ball-Berry and Leuning models produced good fits to the experimental data, and in both cases the optimal minimum canopy conductance $g_0$was relatively small, and thus suggested to simplify Leuning's model by taking g_0 as zero. Based on the simplified Leuning's model, Yu et al. (2001) further proposed to use gross assimilation rate instead of net assimilation, and correspondingly use C_a to replace $C_a - \Gamma$, because stomatal conductance could increase immediately with increasing light even below the light compensation point. Next, by taking humidity response parameter D_0 as 1.5 kpa (Leuning 1995), the Leuning's model shows the following approximation:

$$g_s \sim a_1 \frac{A}{C_a \times (1 + D/1.5)}, \quad (2)$$

Many other studies, however, showed better results when f (D) = $D^{-1/2}$ was used for humidity response than a hyperbolic function of D. It is interesting to note when replacing D with a form of $D^{-1/2}$, the Leuning's modified Ball-Berry's photosynthesis model shows a similar

approximation for the function of *A*, C_a and *D*, as the RuBP regeneration limitation optimization model does.

2. Optimization model for RuBP regeneration limitation

CO_2 fixation can be limited by Rubisco kinetics or by the regeneration of RuBP or co-limited by both. Here we tested two model solutions derived from optimal stomatal theory as shown in Vico et al. (2013). The first model assumed that stomatal aperture was optimized under RuBP regeneration, and the atmospheric CO_2 concentration was much larger than the CO_2 compensation point (i.e., $c_a \gg \Gamma$) and $c_a \gg a\lambda D$ ($a = 1.6$, λ is the marginal water use efficiency). Based on this assumption, Medlyn et al. (2011) derived the following approximation on the left for the optimal stomatal conductance, and Vico et al. (2013) further simplified the equation to obtain the approximation on the right (Vico et al. 2013) :

$$g_s \sim \frac{A}{c_a\sqrt{D}} a\left(\sqrt{D} + \sqrt{\frac{3\Gamma}{a\lambda}}\right) \sim \frac{A}{c_a\sqrt{D}}\sqrt{\frac{3a\Gamma}{\lambda}}, \quad (3)$$

where Γ is the CO_2 compensation point.

3. Optimization model for Rubisco limitation

The second model was derived by Katul et al. (2009) assuming that stomatal aperture was optimized under Rubisco limitation only, and $c_a \gg \Gamma$, so the following linear dependence of stomatal conductance can be found (Vico et al. 2013):

$$g_s \sim \frac{A}{c_a\sqrt{D}}\sqrt{\frac{c_a}{a\lambda}}, \quad (4)$$

We re-arranged equation (4) and obtained the following expression:

$$g_s \sim \frac{A}{\sqrt{c_a D}}\sqrt{\frac{1}{a\lambda}}, \quad (5)$$

Assuming that λ is constant, the relations of equation (3) and (5) show that the g_s could be linearized with the function of C_a, *A*, and *D*, with the slopes of the lines being proportional to

$(3a\Gamma/\lambda)^{1/2}$ for RuBP regeneration limited model and $(a\lambda)^{-1/2}$for Rubisco limited model. Although λ may vary with environmental conditions for long-term (monthly to seasonal scale), in practice, λ can often be considered constant for short term (i.e., sub-hourly to daily) exposure to changing environmental conditions (Vico et al. 2013).

2.2 Testing Data Sets

The model evaluation is based on an analysis of data obtained from various experiments in which changes in stomatal conductance were measured under acclimation of atmospheric CO_2 concentrations under different environmental conditions. A comprehensive literature search using the terms 'CO_2 acclimation', 'stomatal conductance', 'FACE', 'growth chamber' was conducted across Thomson Reuters Web of Science and Google Scholar databases. All of the data used in this study was derived from *in-situ* experiments that examined stomatal conductance responses to different atmospheric CO_2 levels.

Three types of field measurements were used to evaluate the performance of the three photosynthesis models. The conditions to be tested included: (1) the instantaneous measurement of g_s and atmospheric CO_2 concentration (here after C_a), (2) the measurement of g_s and C_a from semi-controlled plant growth facility, and (3) the Free-Air CO_2 Experiment (FACE) measurement of g_s and C_a. We noted that f*(A, C_a, D)* values calculated for Rubisco simulation ranged about 10 times different from f*(A, C_a, D)* values calculated for Leuning's modified model and RuBP model. For a better comparison by using a common scale for all figures, we re-adjusted the x-axis (i.e., f*(A, C_a, D)*) for Rubisco simulation, to scale it to the same range of f*(A, C_a, D)* as those of Leuning's modified Ball-Berry model and RuBP limited model. Such adjustments do not change the slope and R^2 values of f*(A, C_a, D)* and g_s correlation for the Rubisco model.

In the instantaneous g_s measurements, each chamber measurement was made over a short period in the field and the environmental conditions were kept constant. For example,

Yu et al. (Yu et al. 2004) conducted leaf gas exchange measurements in a winter wheat cropping system at North China Plain. In that experiment, the C_a was varied from 0 to 1000 μmol mol^{-1} in the leaf chamber to get instantaneous g_s response to CO_2, while temperature, humidity and wind speed over the leaves were kept constant.

For semi-controlled conditions, the steady-state leaf gas-exchange was measured at a semi-controlled plant growth facility that allowed the study of the effects of elevated CO_2 on the growth of plants under radiation and temperature conditions similar to the field (Anderson et al. 2001, Maherali et al. 2002). Only a few studies have investigated the stomatal acclimation to CO_2 under semi-controlled conditions. Through an extensive literature search, five semi-controlled measurement data sets were extracted from the literature and analyzed (Table S1).

Much of the FACE studies compared g_s responses of plants grown under ambient C_a with those grown under doubled CO_2 concentration. In the FACE experiments, the environmental factors such as leaf temperature and atmospheric water vapor pressure entering the chamber were not controlled during measurements but g_s was measured when it reached steady state. The FACE synthesis was built on the original dataset by Ainsworth and Rogers (2007), and was updated to include the up-to-date database of FACE studies. A total of 48 studies are included in this FACE synthesis, corresponding to 41 different plant species or growing conditions, and CO_2 concentrations ranging from 330 to 757 μmol mol^{-1} (Table S1). These studies were listed in Table S1, and included twenty-one datasets for C_3 herbaceous crops, nine datasets for C_3 grasses, seven datasets for C_3 shrubs, seventeen datasets for C_3 trees, four datasets for C_4 herbaceous crops and four datasets for C_4 grasses.

In addition, we classified the study locations as "dryland" based on an aridity index database following the United Nations Environment Program (UNEP) terminology, in which drylands are defined as regions where the Aridity Index (AI) is smaller than 0.65 (e.g., Wang

et al. 2012), with AI expressed as the ratio of mean annual precipitation to mean annual potential evapotranspiration.

2.3 Parameter Sensitivity Analysis

There are three major factors in equations (2), (3) and (4) controlling g_s: assimilative rate (A), CO_2 concentration (C_a), and vapor pressure deficit (D). In this study, a sensitivity analysis was conducted to examine which parameter (input) could have the most influence on the modeled g_s output, by varying one parameter over its entire observed range while fixing others (i.e., no interactive effects were tested). For the sensitivity analyses, the mean values derived from the entire database were used as the "base case", and the base values were increased and decreased by 1% increment to reach the boundary values (i.e., maximum and minimum values derived from the entire database). The percent change in the model output was calculated (Li et al. 2016). The average of the difference in percentage change between two consecutive g_s output values was then defined as the parameter's sensitivity, which can be described as:

$$Sensitivity = \frac{\sum_{i=1}^{n} \Delta g_{s(i)}}{n} \times 100\%, \quad (5)$$

where $\Delta g_{s(i)}$ is the percentage change of stomatal conductance corresponding to one interval increment in one parameter (e.g., 1% increment was used in this study), n is the number of intervals.

3 Results and Discussion

3.1 Sensitivity Analysis

The sensitivity values for C_a and D were negative while the assimilative rate A had the positive values (Table 1). Sensitivity analyses suggested that the assimilative rate A was the most influential factor among all the parameters for all three models, with an average

sensitivity value of 1.68% (Table 1). The average sensitivity values for C_a and D varied among the different models. C_a exhibited the same sensitivity value of -1.25% for Leuning's modified Ball-Berry model and RuBP limited model, while the Rubisco limited model had a lower average sensitivity value of -0.63% (Table 1). D had the lowest sensitivity values for all of the three models, ranging from -0.57% to -0.64% (Table 1). The results suggested that A and C_a were two main parameters controlling the model output for Leuning's modified Ball-Berry model and RuBP limited model, while the model output for Rubisco limitation was more controlled by A and less controlled by C_a and D. All three models were less sensitive to the parameter D.

3.2 Evaluation of model performance under different environmental conditions

Figure 1 shows the response of g_s to the function of C_a, A, and D, as predicted by the Leuning's modified Ball-Berry model and the two single-limitation optimization models. The results of Figure 1 are based on the instantaneous measurement data. The response of g_s to the function of C_a, A, and D were better predicted by Leuning's modified Ball-Berry model and RuBP limited optimization model, with a R^2 value of 0.78 for Leuning's modified Ball-Barry model ($p < 0.05$), and 0.81 for RuBP-limited optimization model ($p < 0.05$) (Fig. 1). However, the Rubisco-limited optimization model could not predict the response of g_s well with the function of C_a, A, and D, showing a low R^2 value of 0.21 ($p < 0.05$) (Fig. 1).

None of the three models showed a good performance to predict the response of g_s to the function of C_a, A, and D using the semi-controlled measurement data (Fig. 2). The predictability of g_s using the function of C_a, A, and D were low for all the three models, with R^2 values ranging from 0.21 to 0.31 ($p < 0.05$) (Fig. 2). However, there was significant difference between functional groups. The predictability of g_s was significantly improved when separating functional groups. The Leuning's modified Ball-Berry model and the RuBP-limited optimization model provided R^2 values of 0.56 and 0.54 ($p < 0.05$) for C_3 species, and

R^2 values of 0.67 and 0.58 ($p < 0.05$) for C_4 species, respectively (Fig. 3). The Rubisco-limited optimization model, however, showed much better g_s predicting power for C_4 species ($R^2 = 0.67$, $p < 0.05$) than C_3 species ($R^2 = 0.19$, $p < 0.05$) (Fig. 3). Besides the difference in functional groups, it was found there was a significant difference between annual and perennial species. The g_s can be better predicted by the function of C_a, A, and D for the annual species alone, with a R^2 value of 0.68, 0.72, and 0.58, for Leuning's model, RuBP limited model and Rubisco limited model, respectively ($p < 0.05$) (Fig. 4). In comparison, the g_s predictability on perennial species was much lower, with a R^2 value ranging between 0.25 and 0.36 ($p < 0.05$) (Fig. 4). This may imply that g_s is less sensitive to C_a, A, and D for perennial species than annual species.

Because the environmental factors such as atmospheric water vapor pressure were not monitored in FACE experiments, only the estimates of g_s as the function of C_a and A were tested for FACE data. In general, none of the three models provided a good estimate of g_s as the function of C_a and A on either C_3 plants or C_4 plants when combining herbaceous and woody species using the FACE data (Fig. 5). But a detailed analysis of the FACE database used for this study indicated that there was significant variability among functional groups regarding the g_s response to elevated CO_2 (Fig. 6). On average, $g_s$was reduced by 21.7%, 22.2%, 13.5%, 16.6%, 30.5%, and 32.3% in C_3 herbaceous crops, C_3 grasses, C_3 shrubs, C_3 trees, C_4 herbaceous crops, and C_4 grasses, with an atmospheric CO_2 enhancement of 54%, 66%, 59%, 54%, 52%, 81%, respectively. Trees and shrubs showed a lower percentage decrease in g_s compared to C_3 and C_4 grasses and crops, similar to the trend reported previously (Saxe et al. 1998, Nowak et al. 2004, Ainsworth and Rogers 2007). When separating into different plant life forms (e.g., trees, shrub or grasses), the predicted linear correlation of g_s and the function of C_a and A on trees and shrubs had been considerably improved with R^2 value rising to 0.70, 0.70 and 0.65 for C_3 trees ($p < 0.05$), 0.87, 0.87 and

0.82 for C_3 shrubs ($p < 0.05$), on linear fitting with Leuning's modified Ball-Berry model, RuBP limited model, and Rubisco limited model, respectively (Fig. 6). But crops and grasses still had low R^2 value for the g_s dependence on the function of C_a and A (Fig. 6). It was noted that g_s might be better predicted by the function of C_a and A for the perennial species than for the annual species (Fig. 7). Although the result seemingly contrasted with what was observed from semi-controlled data, a detailed data check revealed that the majority of annual species were C_3 and C_4 crops, indicating that functional groups could be a more important factor affecting the model performance as discussed in the later sections.

In general, the Leuning's modified Ball-Berry model and RuBP limited optimization model showed better predictability on g_s response to the function of C_a, A, and D than Rubisco limited model. It is not surprising that Leuning's modified model and RuBP model have exhibited the similar patterns of model projection, since RuBP model was derived structurally homogenous to the classic Ball-Berry model but was based on the optimal stomatal conductance theory (Medlyn et al. 2011). A major difference between these two formulations of g_s was that Leuning's model used a hyperbolic form of D while RuBP limited model used $f(D) = D^{-1/2.}$. Our sensitivity analysis has indicated that model output for Leuning's modified model and RuBP limited model were more sensitive to A and C_a, and less sensitive to D, so the modeled stomatal conductance is less influenced by using the different form of the function D. The RuBP regeneration limited model generally simulated more accurate C_a response because its formulation could predict a stomatal closure to rising C_a for all the values above 200 ppm, while the Rubisco limited formulation predicted that the stomata was to open at rising C_a up to C_a values of 500-600 ppm (Medlyn et al. 2013, Buckley 2017). The current data-driven analytical results generally supported the previous findings, but it is noted that other factors such as functional groups could play a more important role in achieving a better model performance.

The results showed that the Rubisco-limited optimization model could not predict the response of g_s well with the functions of C_a, A, and D, for any types of the field data on C_3 species. This can be explained by what process is limiting A at given CO_2 and whether the control of A shifts from Rubisco and to RubP regeneration as CO_2 arises. For C_3 plants, Rubisco capacity is the predominant limitation on A at low CO_2 while the limitation shift to RuBP regeneration capacity at elevated CO_2 (Long and Drake 1992). Our collected data for C_a ranged between 100 – 998 ppm, particularly, a major part of the C_a from the instantaneous measurements and semi-controlled measurements were within the transition for the stomatal aperture being Rubisco activity to RuBP regeneration. As C_a continued to rise, the photosynthesis on C_3 plants moved towards more predominately limited by RuBP regeneration. To date, the global average concentration of CO_2 in the atmosphere has increased to approximately 405 ppm (Lugokencky 2017), which implies that RuBP limited model maybe give more reasonable prediction. C_4 metabolism behaves under different mechanism in which CO_2 is saturated at low C_a, and A is less sensitive to the increase in C_a (Ghannoum et al. 2000).

Different plant functional types can significantly affect the model performance. Previous studies had indicated that, for C_3 plants, the magnitude of a decrease in Rubisco activity or increase in the capacity for RuBP regeneration varied among the different functional groups. For example, trees have the smallest reduction in Rubisco activity when compared to grasses, crops, and shrubs (Ainsworth and Rogers 2007), while crops could reduce the Rubisco activity at elevated CO_2 to a greater extent than the capacity for RuBP regeneration (Long et al. 2006). The C_4 plants are different because they are CO_2 saturated at current CO_2, and when CO_2 rises, the competitive advantage conferred by C_4 metabolism will be reduced (Sage 2004).

3.3 Evaluation of model performance for dryland data

The CO_2 assimilation models such as Ball-Berry model and Leuning's modified version have proved to work well under conditions of ample water supply. In this study, we are also interested to know whether these models could perform well under water-stressed conditions. Given the limited data available, we tested the performance of Leuning's modified Ball-Berry model and the two optimization models using semi-controlled field measurement data conducted at dryland sites. It is not surprising that neither model provide a good estimation of g_s as the function of C_a, A, and D (Fig. 8). Studies have shown that soil moisture stress may introduce significant uncertainty into the carbon projection and how vegetation responds to water stress in dryland ecosystems causing 40 – 80% of the inter-model variability (Trugman et al. 2018).

We have found that the functional groups and life forms might pose a significant influence on the results. The linear correlation of g_s dependence of the function of C_a and A had been considerably improved when data were separating into different plant and life forms (e.g., perennial C_3 grass or annual C_3 grass) (Fig. 9). The R^2 values generally ranged from 0.65 to 0.90 on linear fitting with Leuning's modified Ball-Berry model and RuBP limited model. However, the predictability of g_s on perennial C_3 herb and annual C_3 grass were still low for Rubisco limited model, with the R^2 values of 0.02 for annual C_3 grass and 0.16 for perennial C_3 herb (Fig. 9). This is consistent with the overall trend as we discussed in the previous section. Studies have demonstrated that plants can increase g_s as a response to rising CO_2 under warm and dry conditions (Purcell et al. 2018). Rubisco-limited formulation predicted that the stomata was to open at rising C_a up to C_a values of 500-600 ppm (Medlyn et al. 2013)., It is interesting, however, Rubsico limited model did not show a good performance for our dryland data.

We have noted, though, all the species tested are C_3 plants, which may further imply that the functional group could be a more important factor affecting the model performance. Depending on which mechanisms (i.e., hydraulic redistribution or using stored water) plants take to adapt to drought, it may largely affect plant stomata response to drought or CO_2. With differences in plants' functional group adaption to drought, the response of stomata to drought or CO_2 may be different (Yu and D'Odorico 2015).

4 Conclusions

In this study, we evaluated the performance of three commonly-used g_s formations to predict the stomatal conductance response to CO_2 enrichment under different environmental conditions. This is one of the first studies that have attempted to test these models using the same set of measurements from various environmental conditions. Although there could be a potential limitation of using leaf level g_s models to test canopy-scale measurements (i.e., FACE data), Leuning's modified Ball-Berry model and RuBP limited optimization model generally provided a good estimates of g_s for all the tested datasets. We have further found that the factors such as functional groups (e.g., C_3 versus C_4 species) and life form (e.g., annual versus perennial species) may play an important role in determining the stomatal response to changes in environmental factors, and therefore need to be explicitly considered in the modeling framework.

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Table 1. Model sensitivity of key parameters for Leuning's modified Ball-Berry model, RuBP limited optimization model, and Rubisco limited optimization model.

		Leuning's modified Ball-Berry model		Optimization model for RuBP limited		Optimization model for Rubisco limited	
Parameters	Step	Interval	Average sensitivity (%)	Interval	Average sensitivity (%)	Interval	Average sensitivity (%)
Assimilative rate *A* (μmol m^{-2} s^{-1})	1%	[1.8, 39.0]	1.68	[1.8, 39.0]	1.68	[1.8, 39.0]	1.68
CO_2 concentration *Ca* (μmol mol^{-1})	1%	[100, 998]	-1.25	[100, 998]	-1.25	[100, 998]	-0.63
Vapor pressure deficit (kPa)	1%	[0.45, 3.2]	-0.57	[0.45, 3.2]	-0.64	[0.45, 3.2]	-0.64

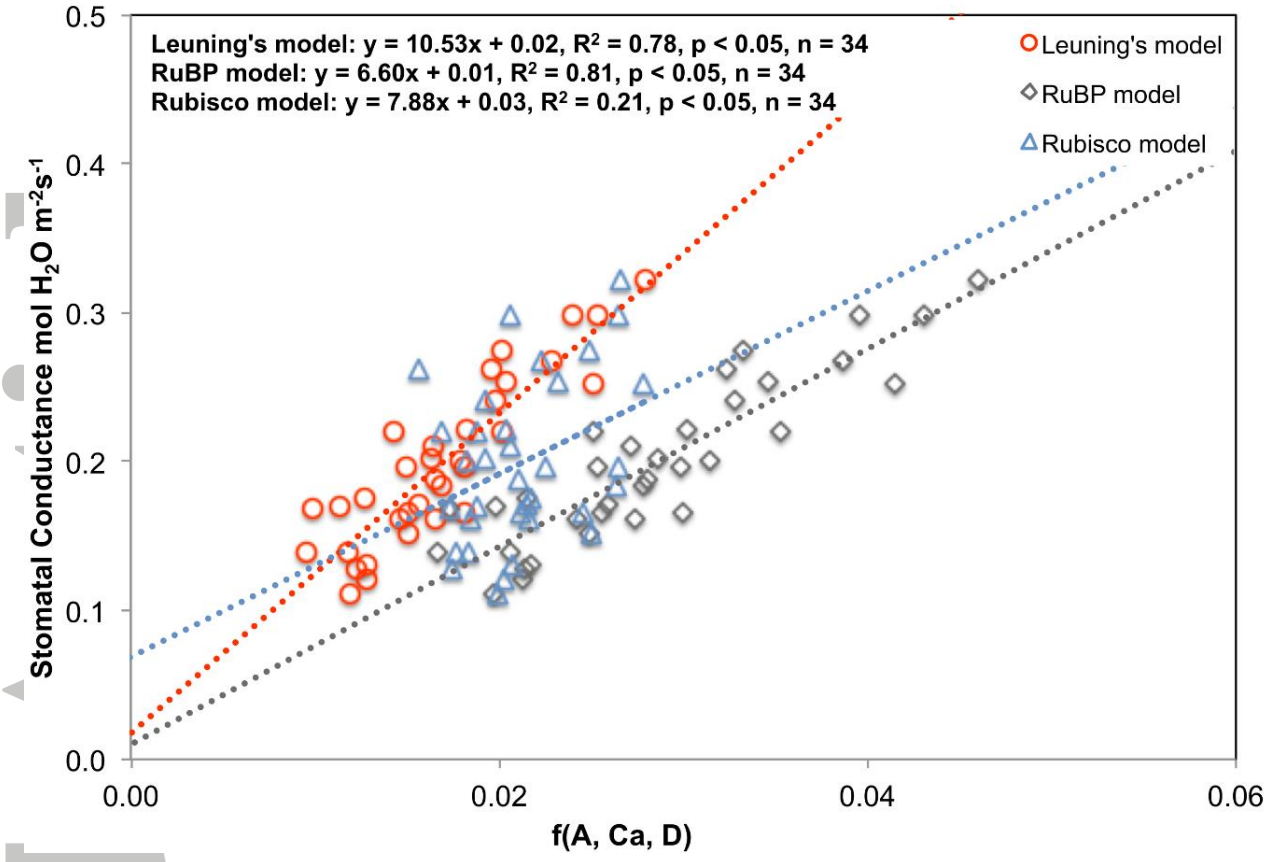


Figure 1. Instantaneous measurements of stomatal conductance g_s as a function of C_a, A, and D for the Leuning's modified Ball-Berry model (red open circles), RuBP limited optimization model (grey open squares), and Rubisco limited optimization model (blue open triangles), with C_a ranging between 200 and 1000 ppm.

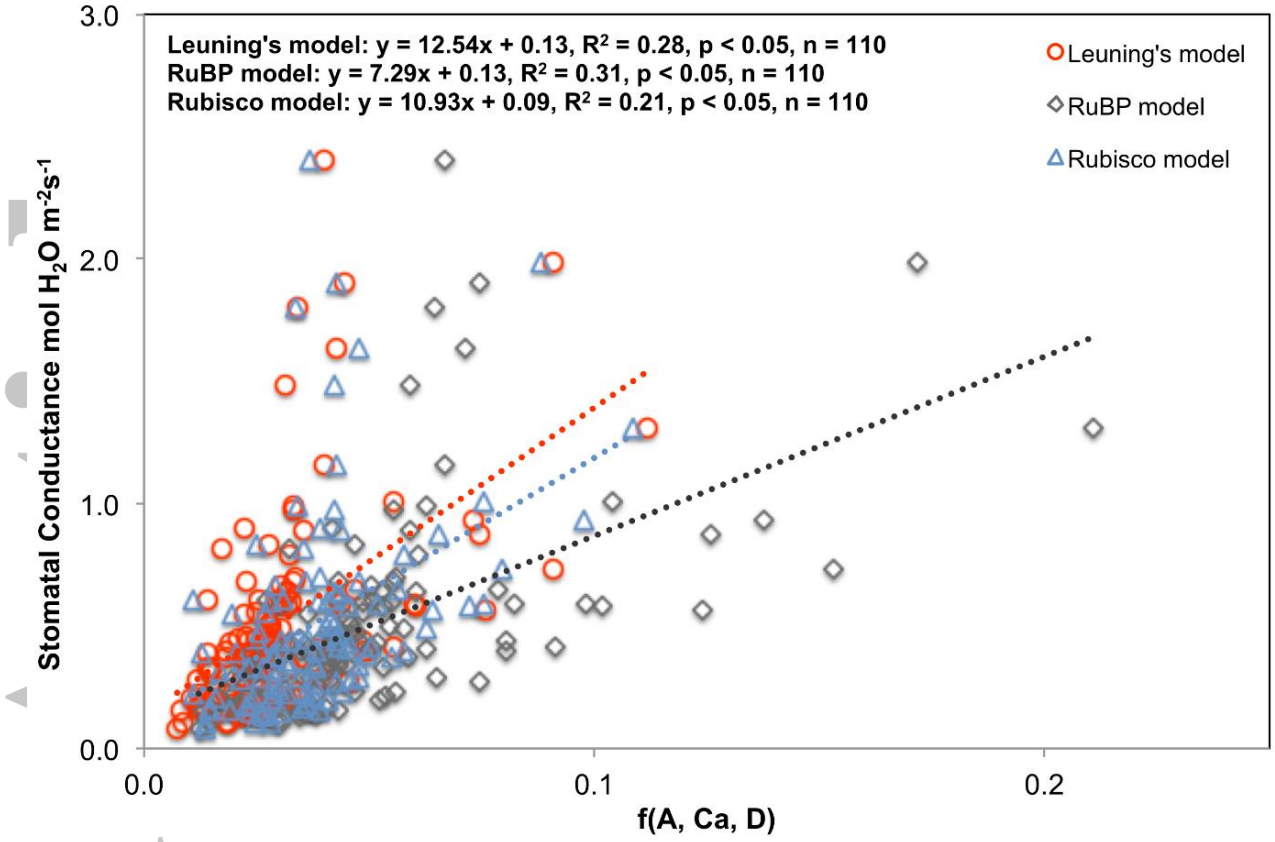
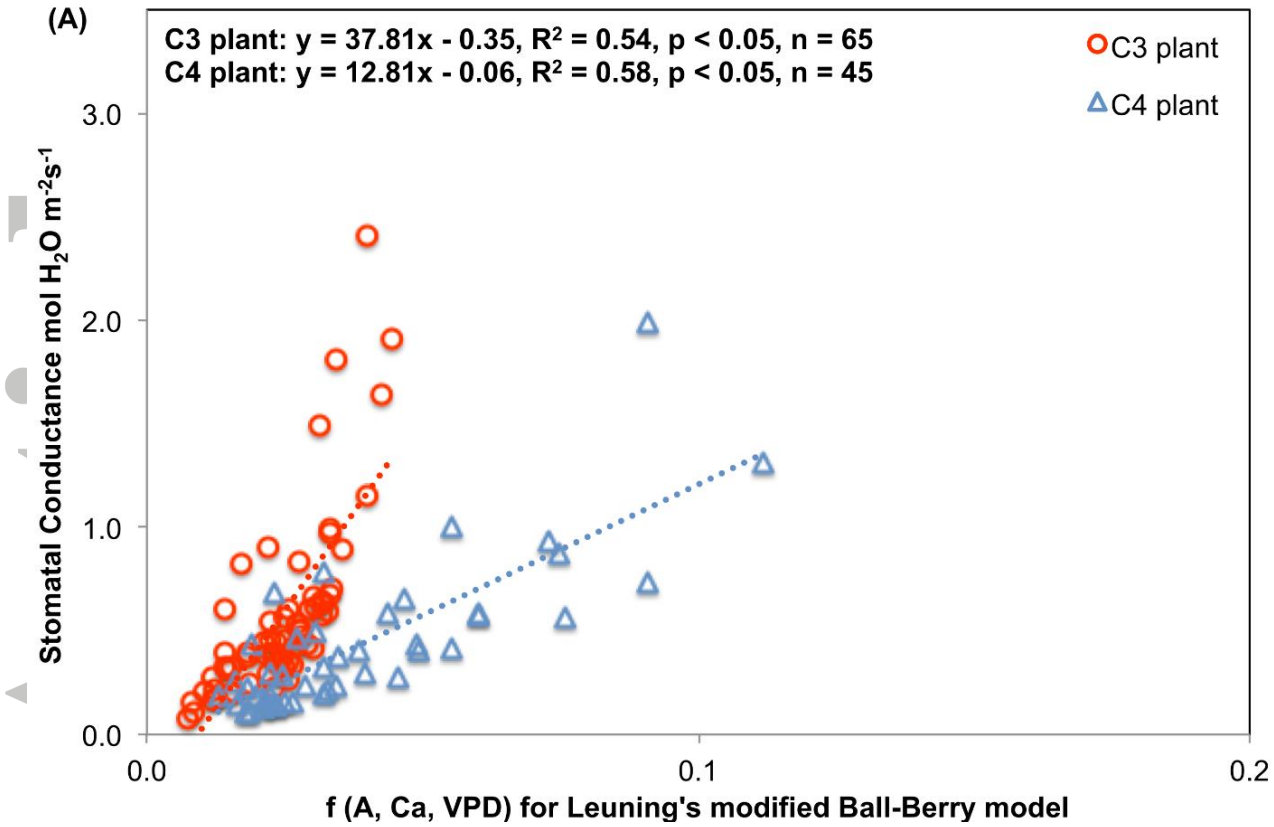
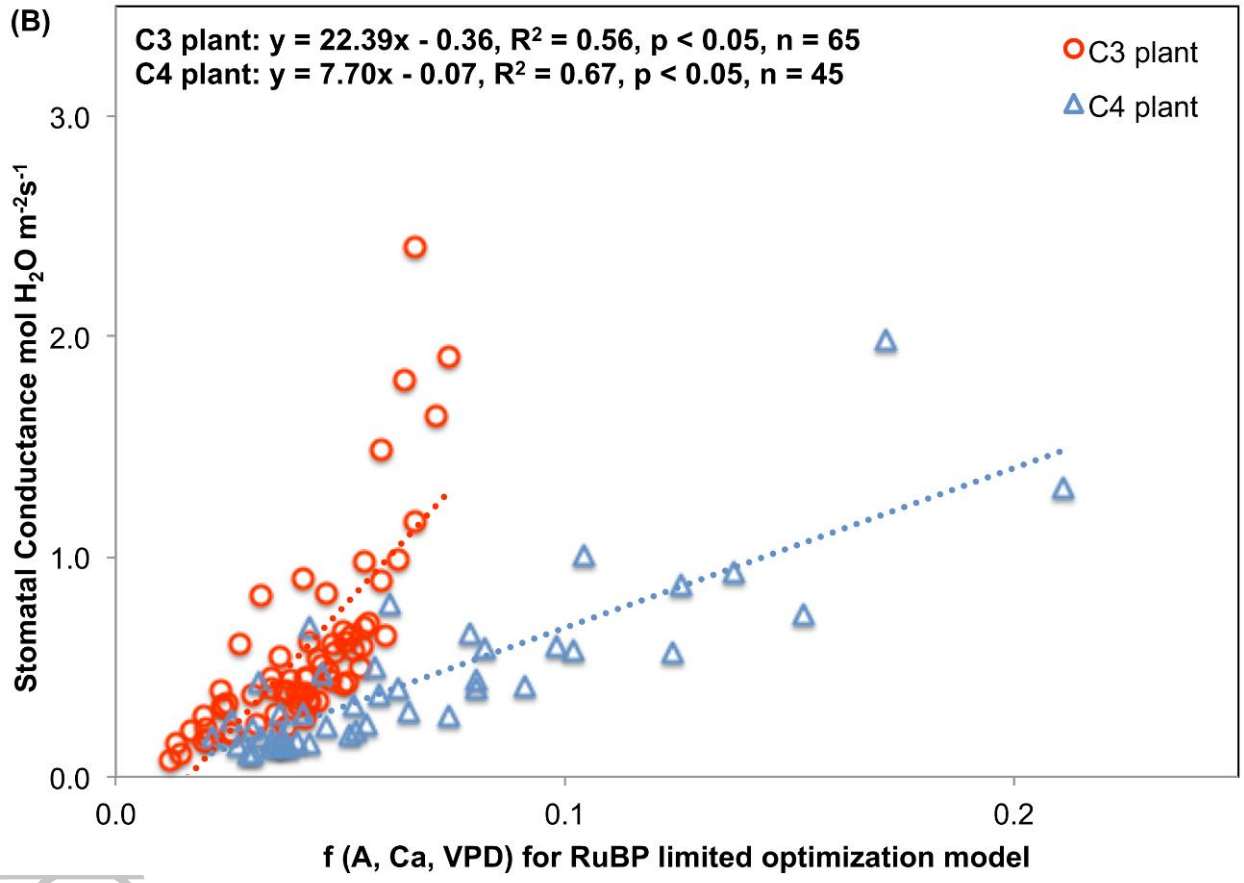


Figure 2. Semi-controlled measurements of stomatal conductance g_s as a function of C_a, A, and D for the Leuning's modified Ball-Berry model (red open circles), RuBP limited optimization model (grey open squares), and Rubisco limited optimization model (blue open triangles).





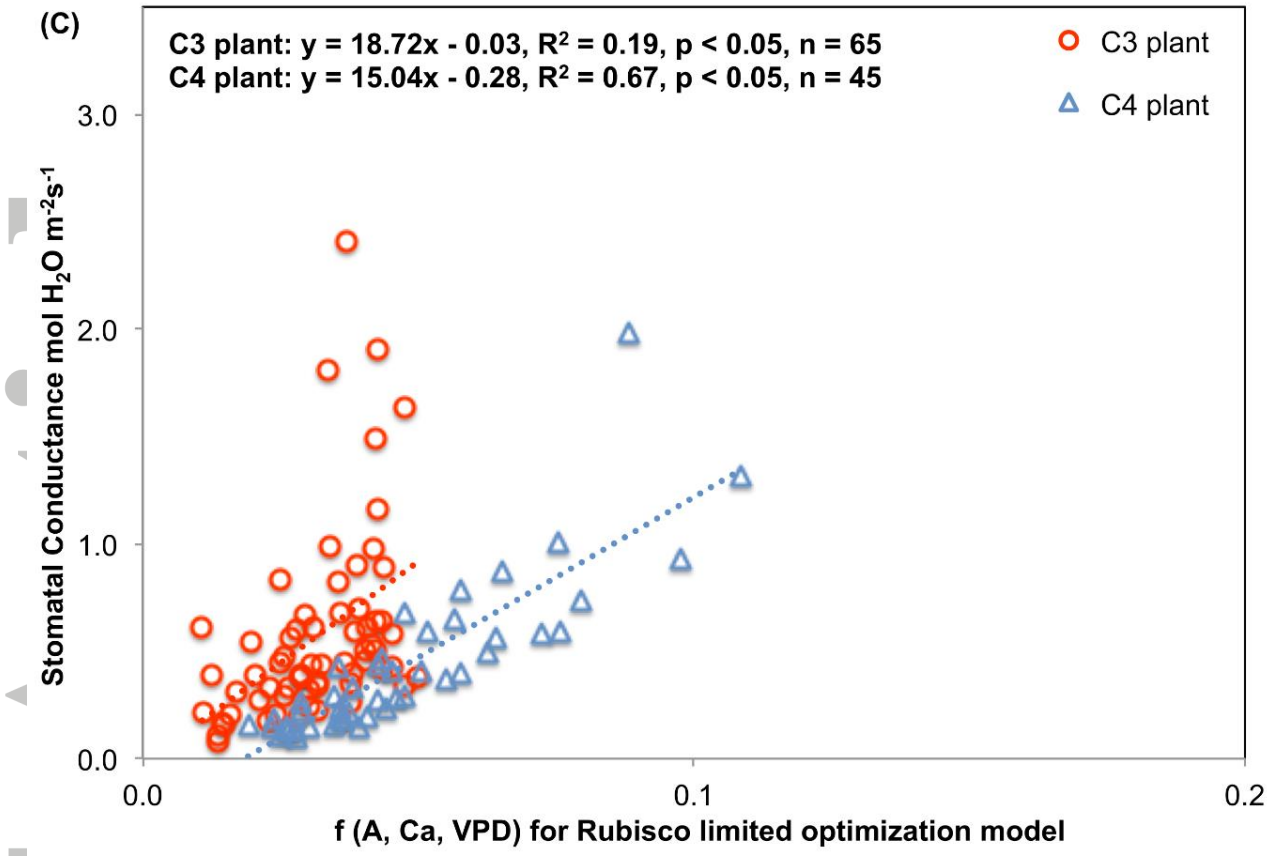
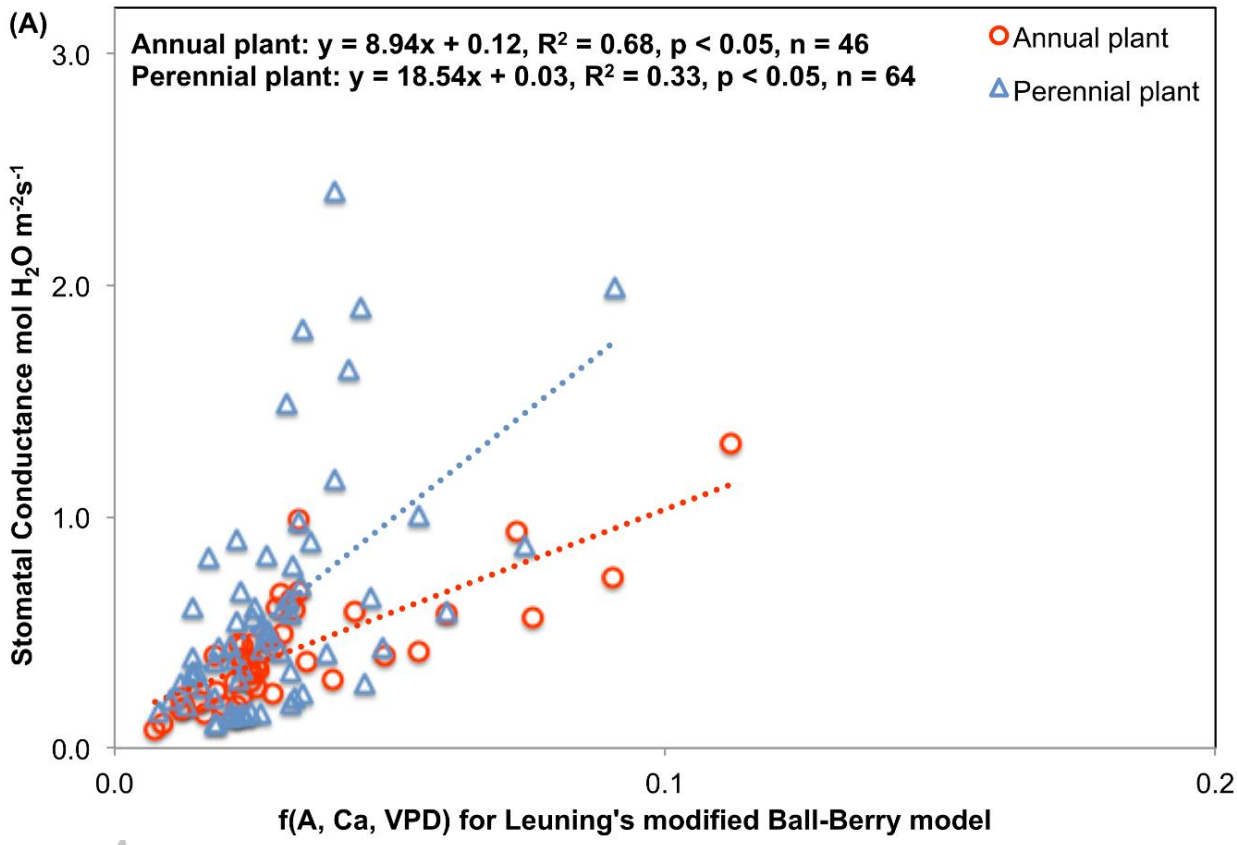
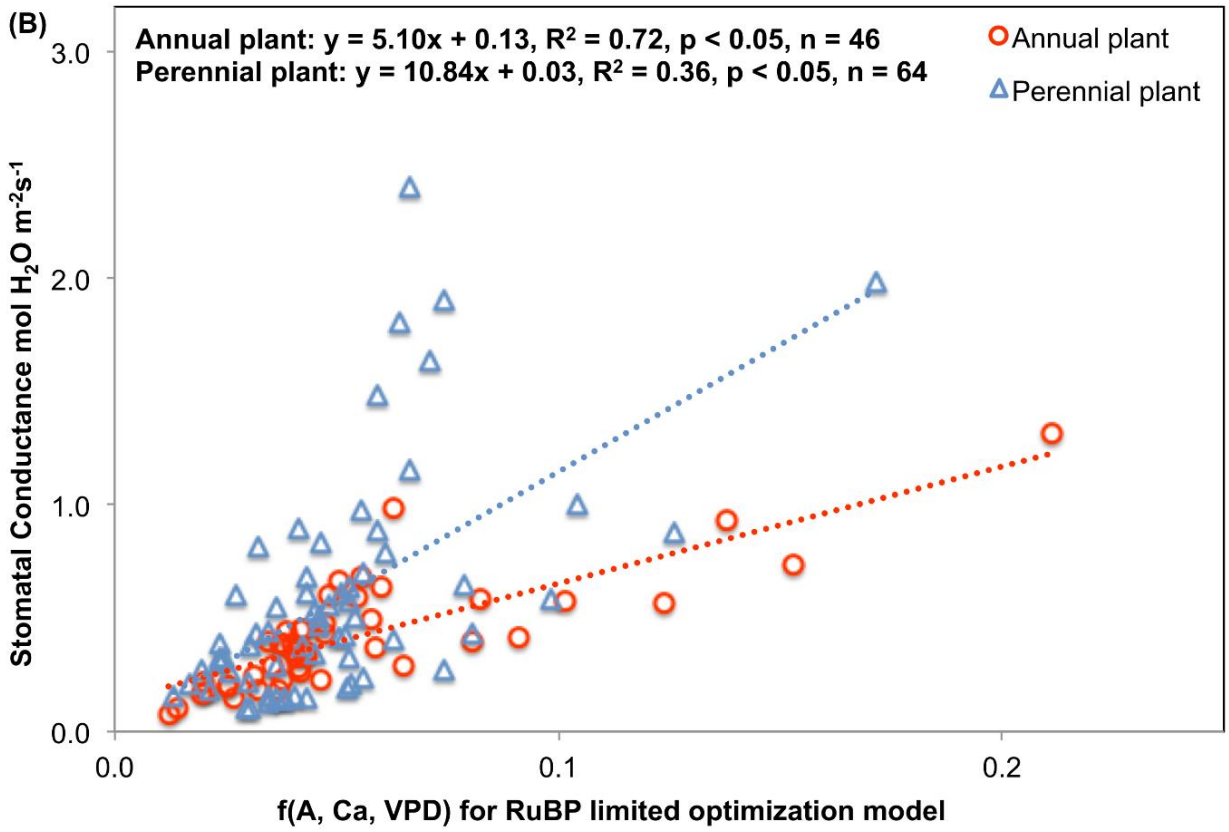


Figure 3. The response of stomatal conductance g_s as a function of C_a, A, and D for two functional groups (C_3 plant vs. C_4 plant), for the Leuning's modified Ball-Berry model (A), RuBP limited optimization model (B), and Rubisco limited optimization model (C). The data are from semi-controlled measurements.





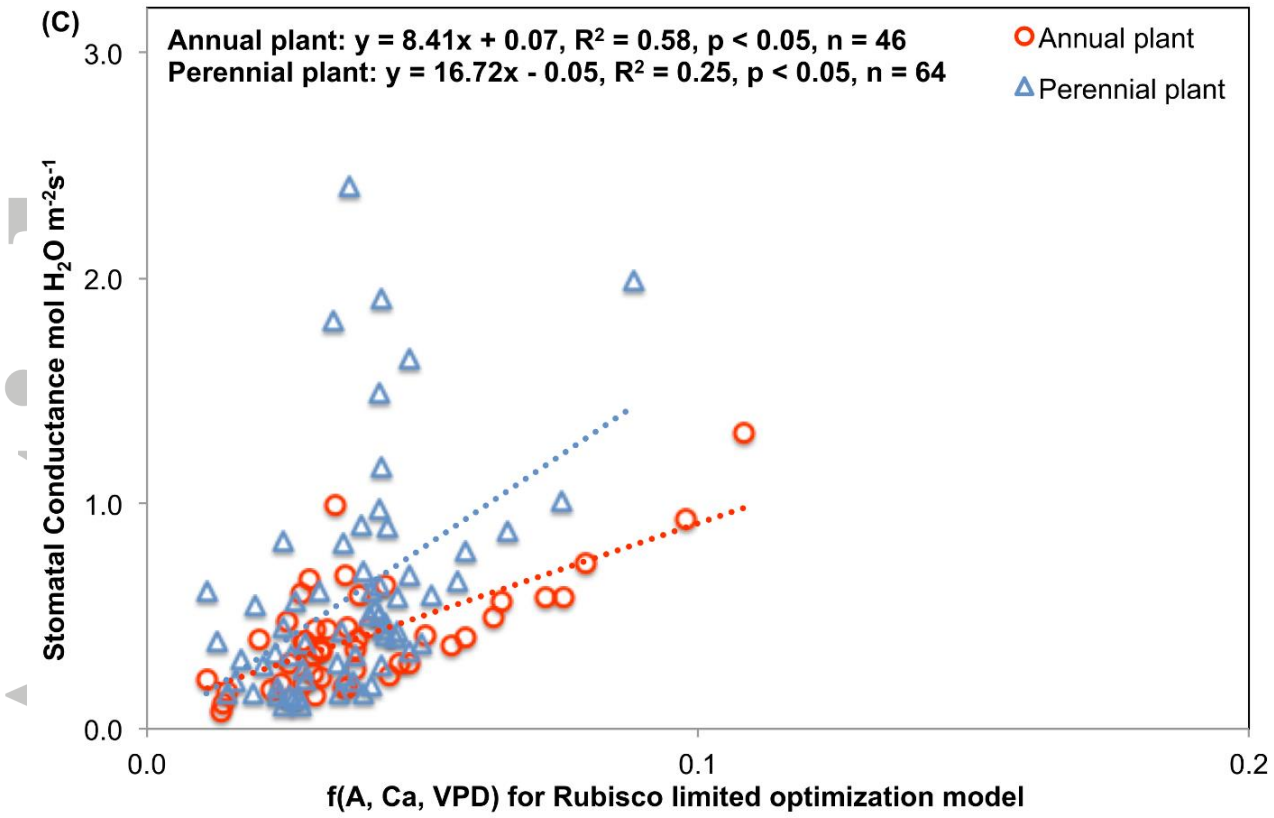
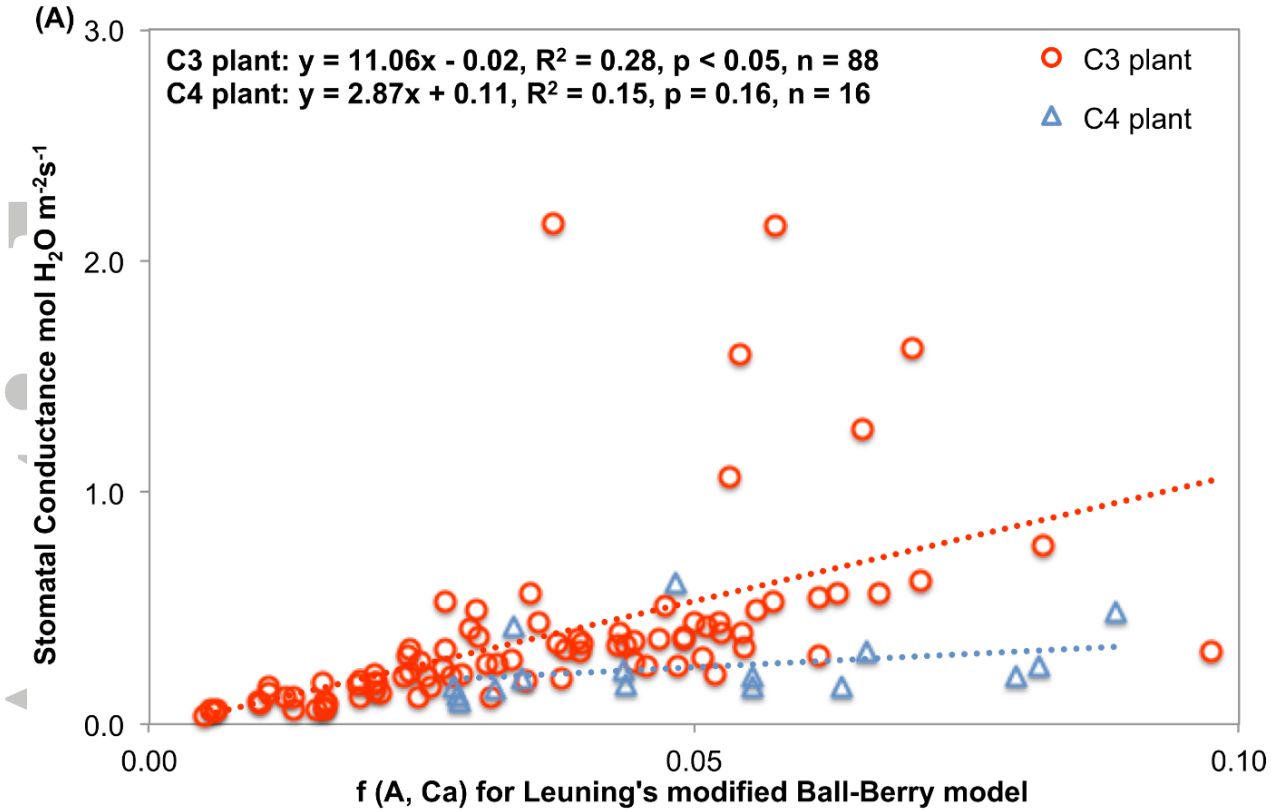
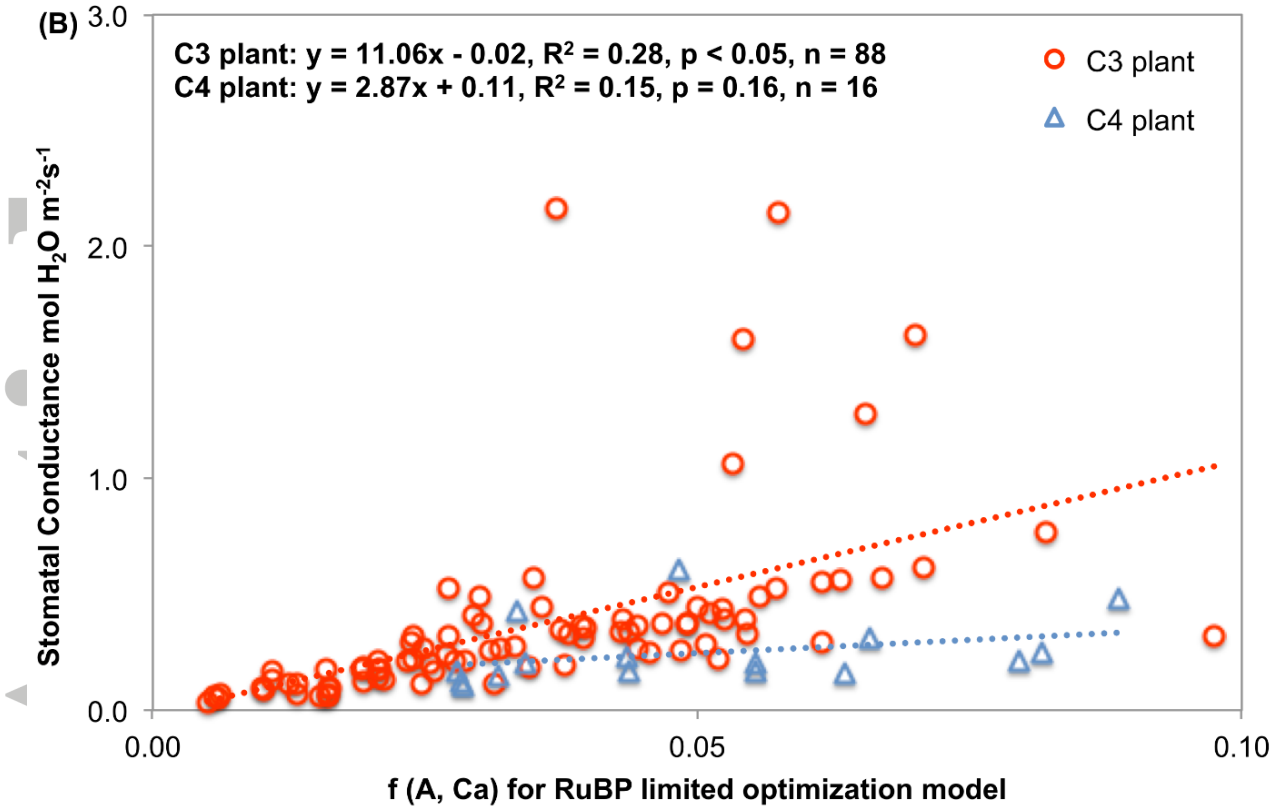


Figure 4. The responses of stomatal conductance g_s as a function of C_a, A, and D for different life forms (annual vs. perennial plant), for the Leuning's modified Ball-Berry model (A), RuBP limited optimization model (B), and Rubisco limited optimization model (C). The data are from semi-controlled measurements.





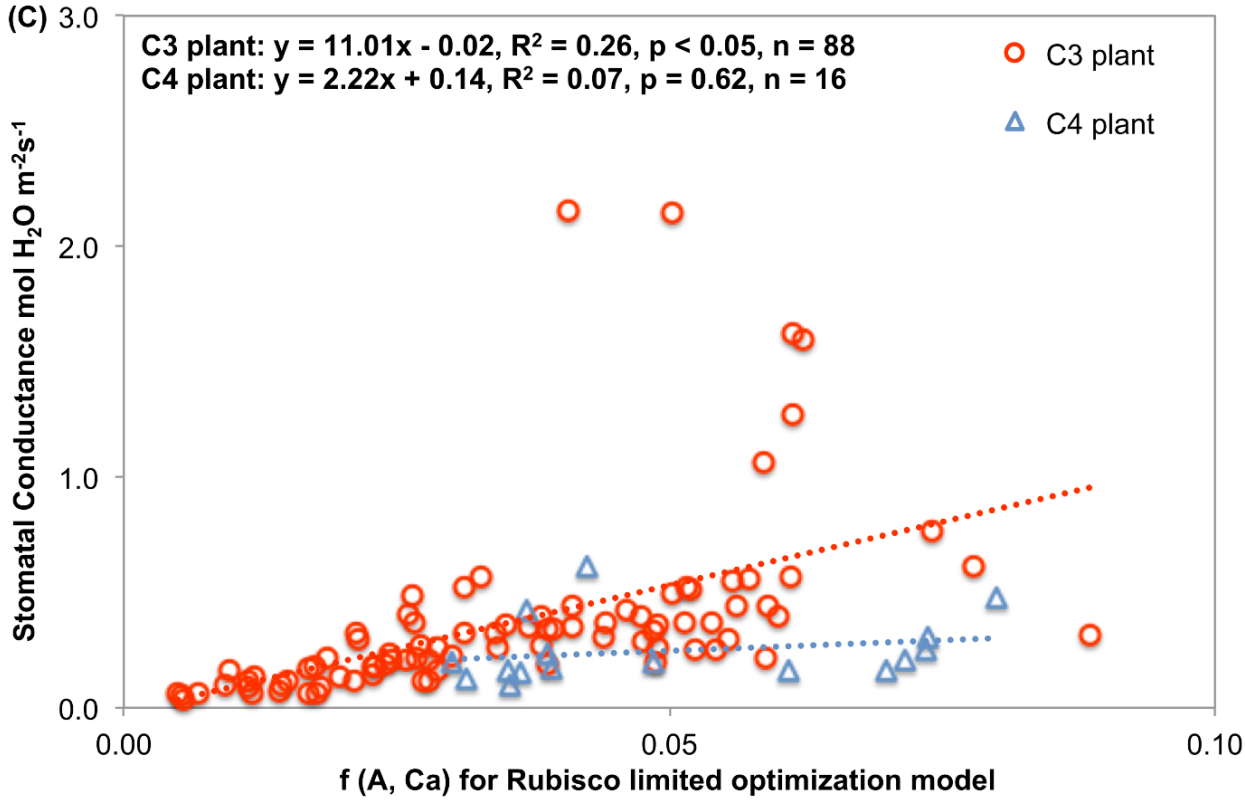
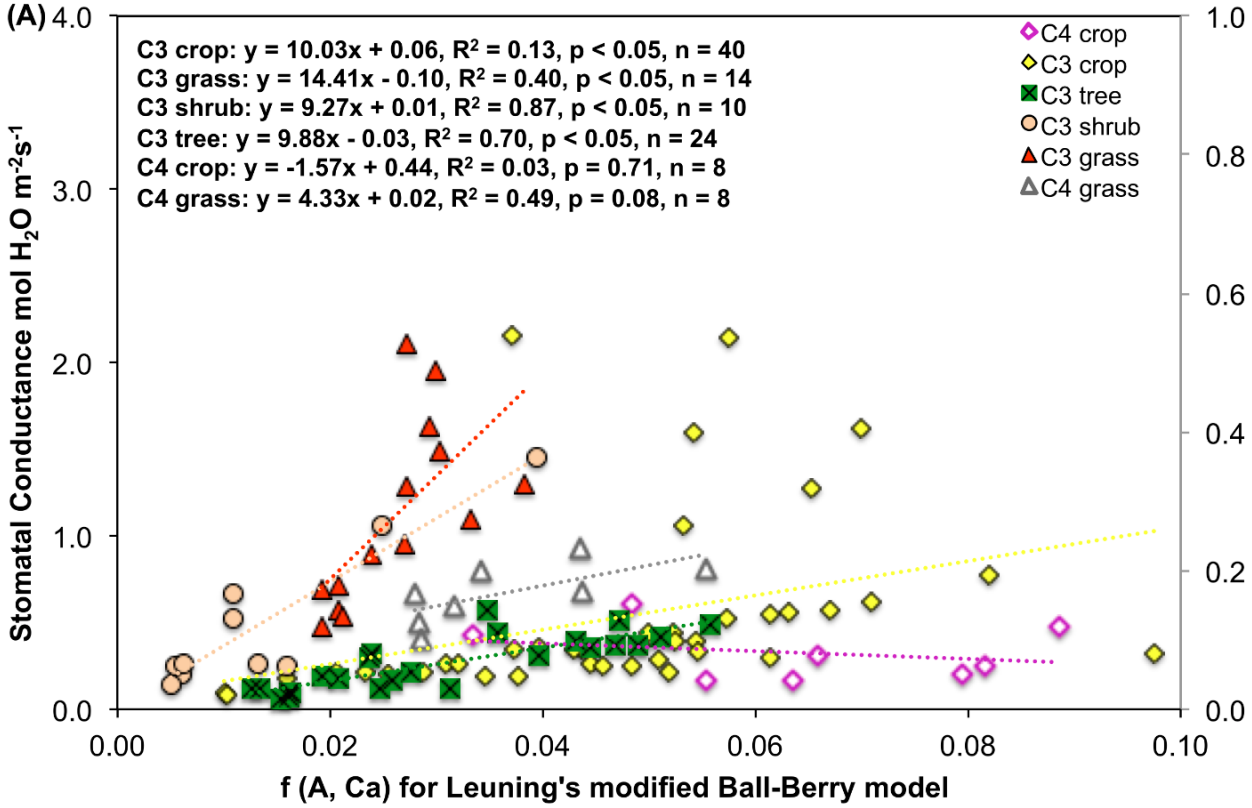
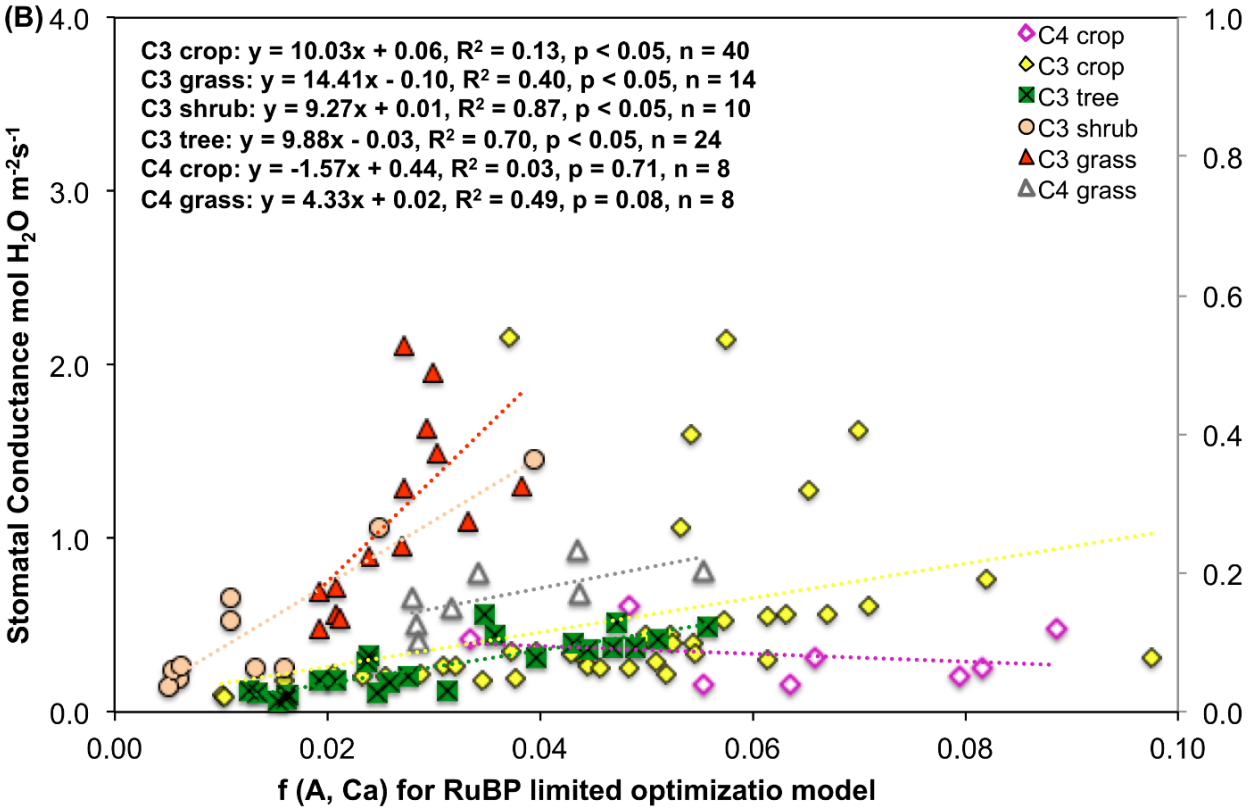


Figure 5. The response of stomatal conductance g_s as a function of C_a and A for the Leuning's modified Ball-Berry model (A), RuBP limited optimization model (B), and Rubisco limited optimization model (C). The data are from FACE measurements.





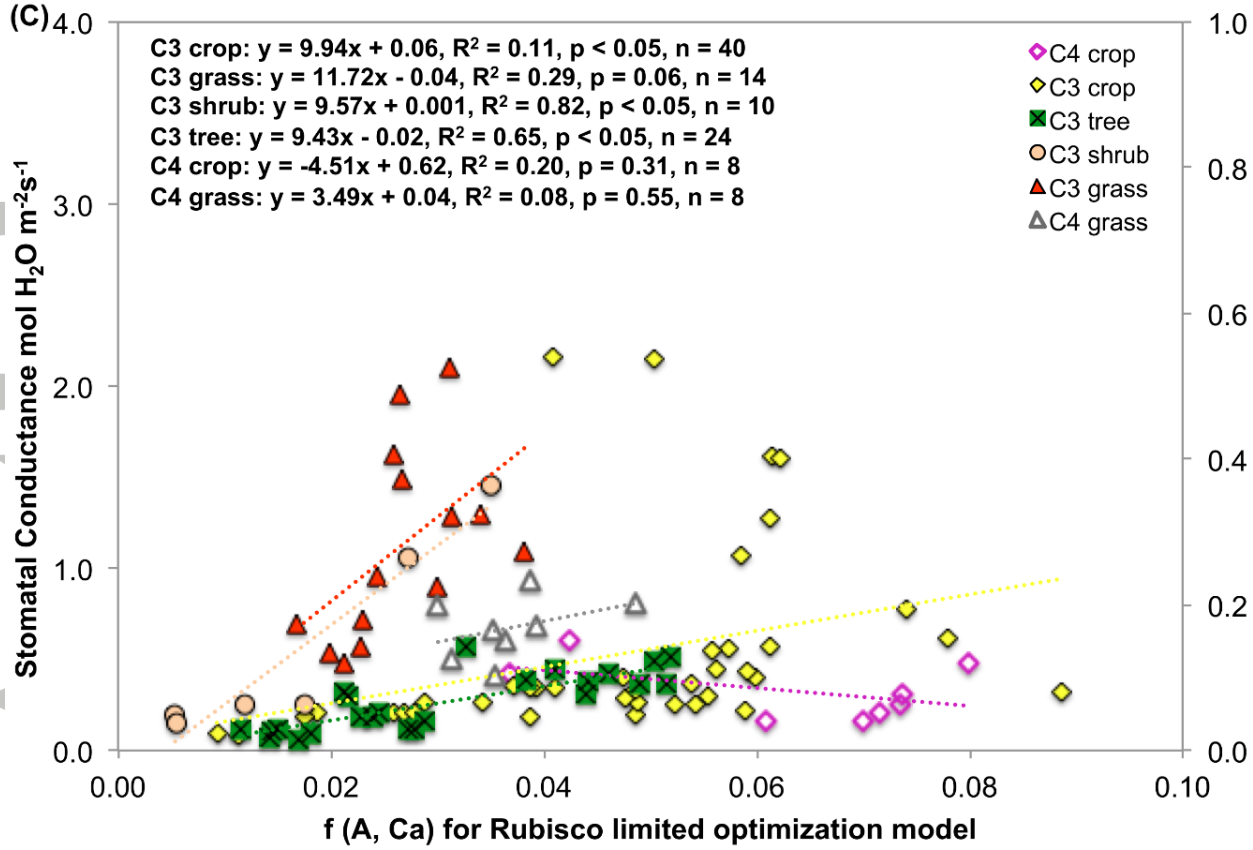
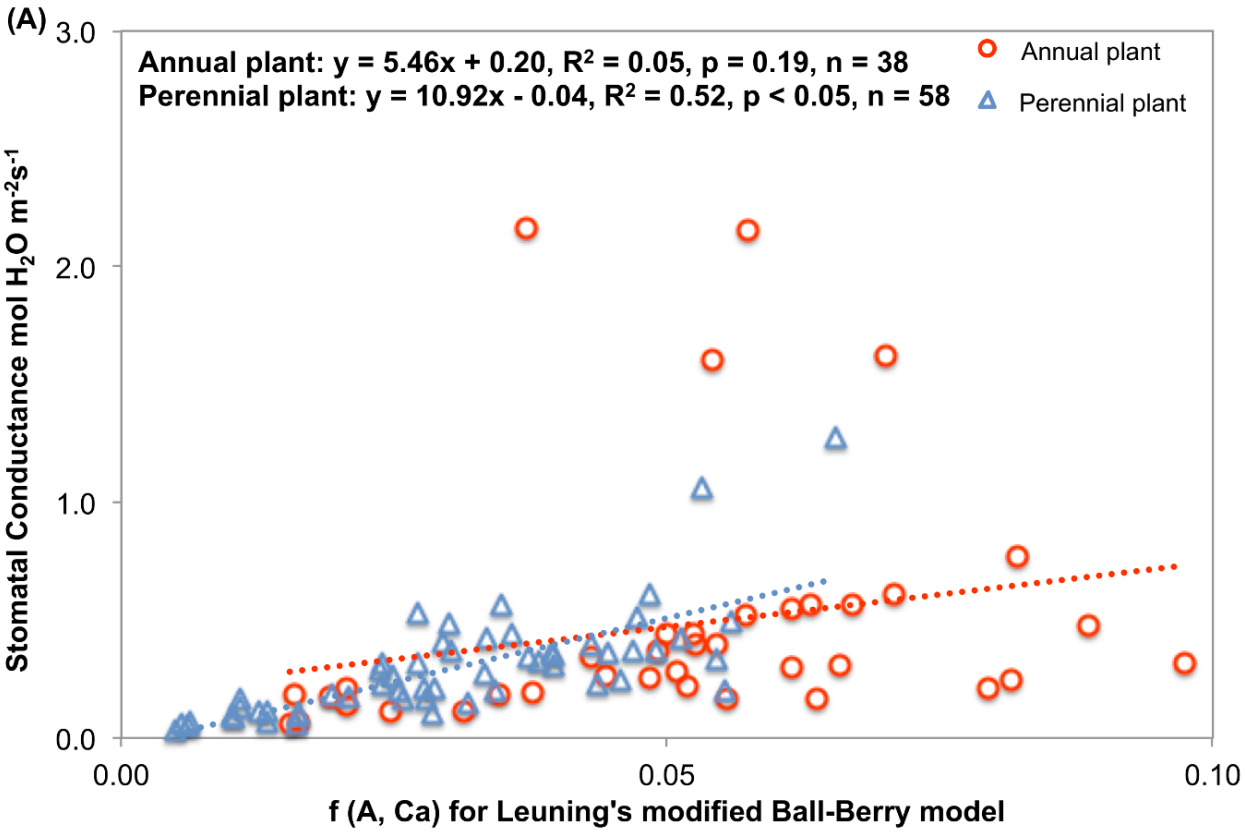
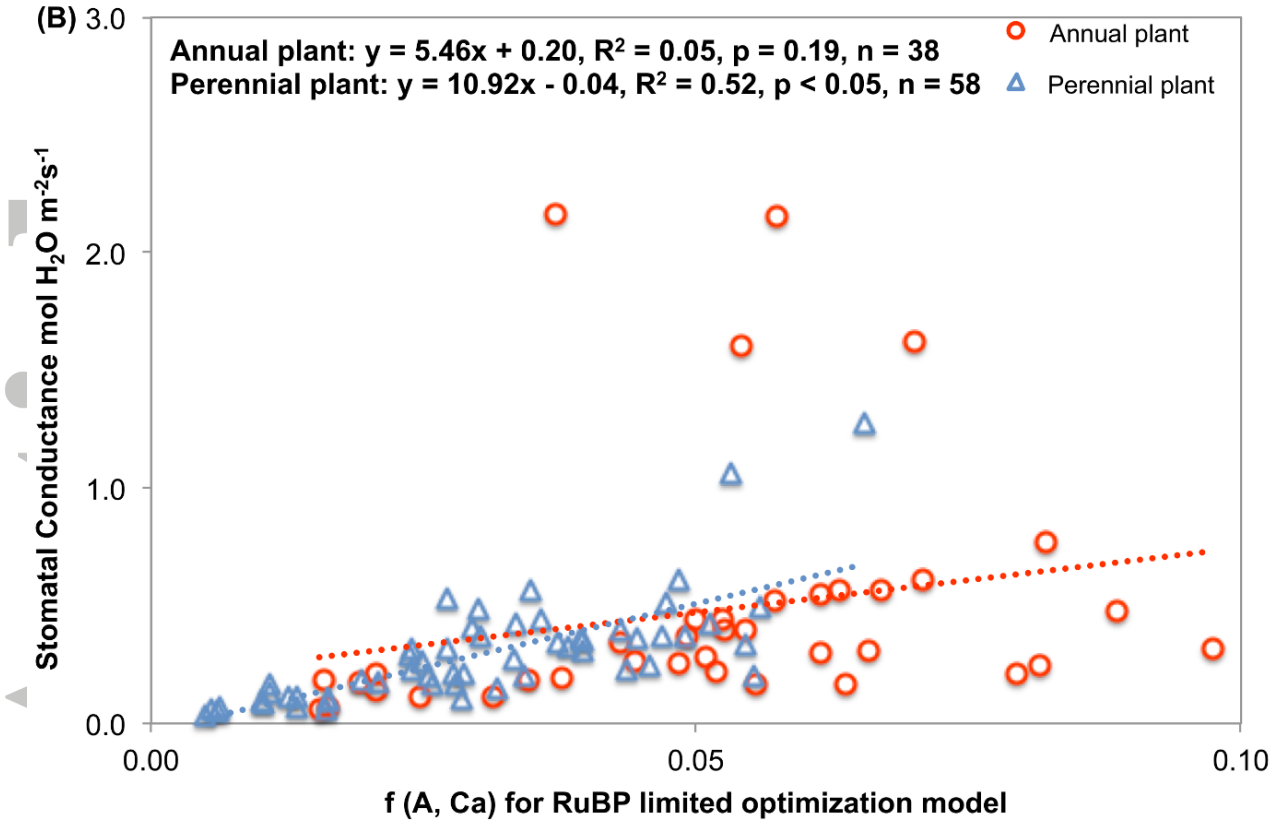


Figure 6. The response of stomatal conductance g_s as a function of C_a and A for different functional groups, for the Leuning's modified Ball-Berry model (A), RuBP limited optimization model (B), and Rubisco limited optimization model (C). The data are from FACE measurements.





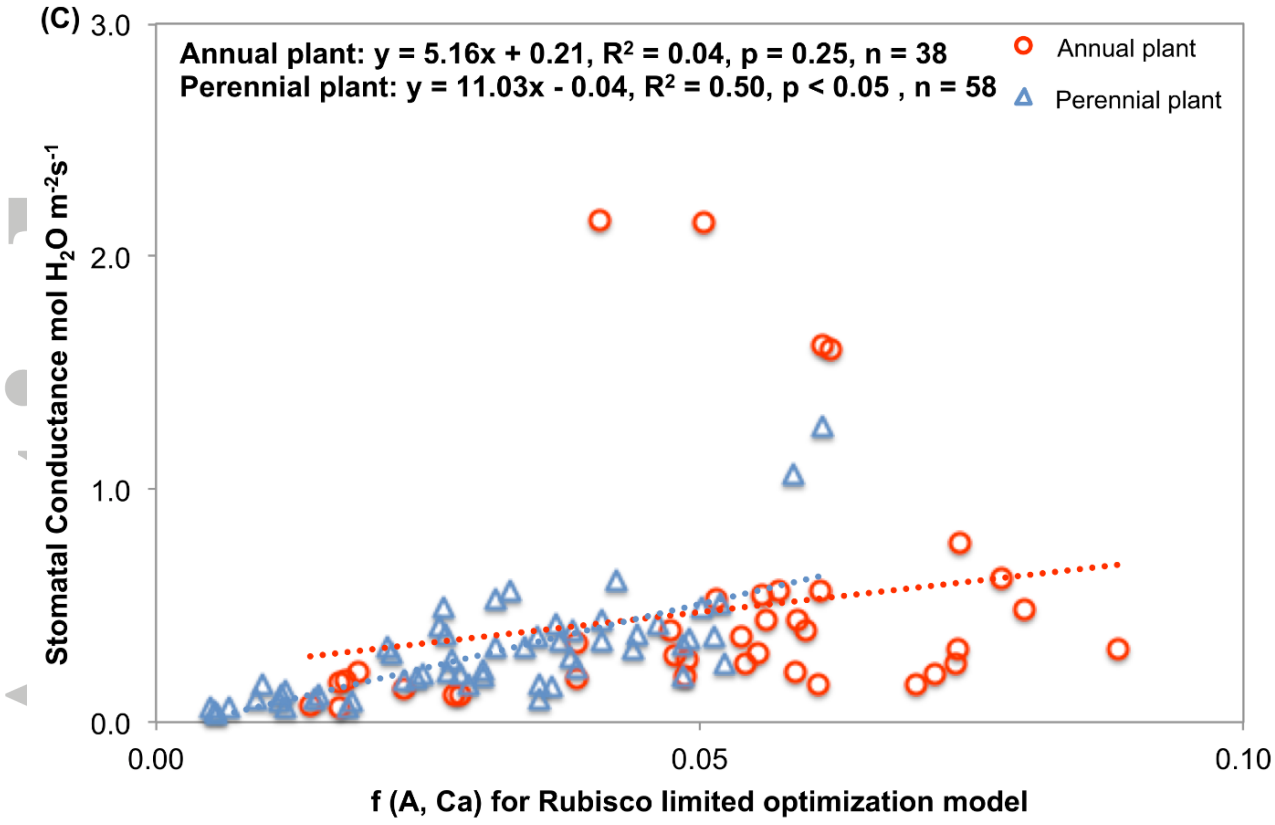


Figure 7. The response of stomatal conductance g_s as a function of C_a and A for different life forms (annual vs. perennial plant), for the Leuning's modified Ball-Berry model (A), RuBP limited optimization model (B), and Rubisco limited optimization model (C). The data are from FACE measurements.

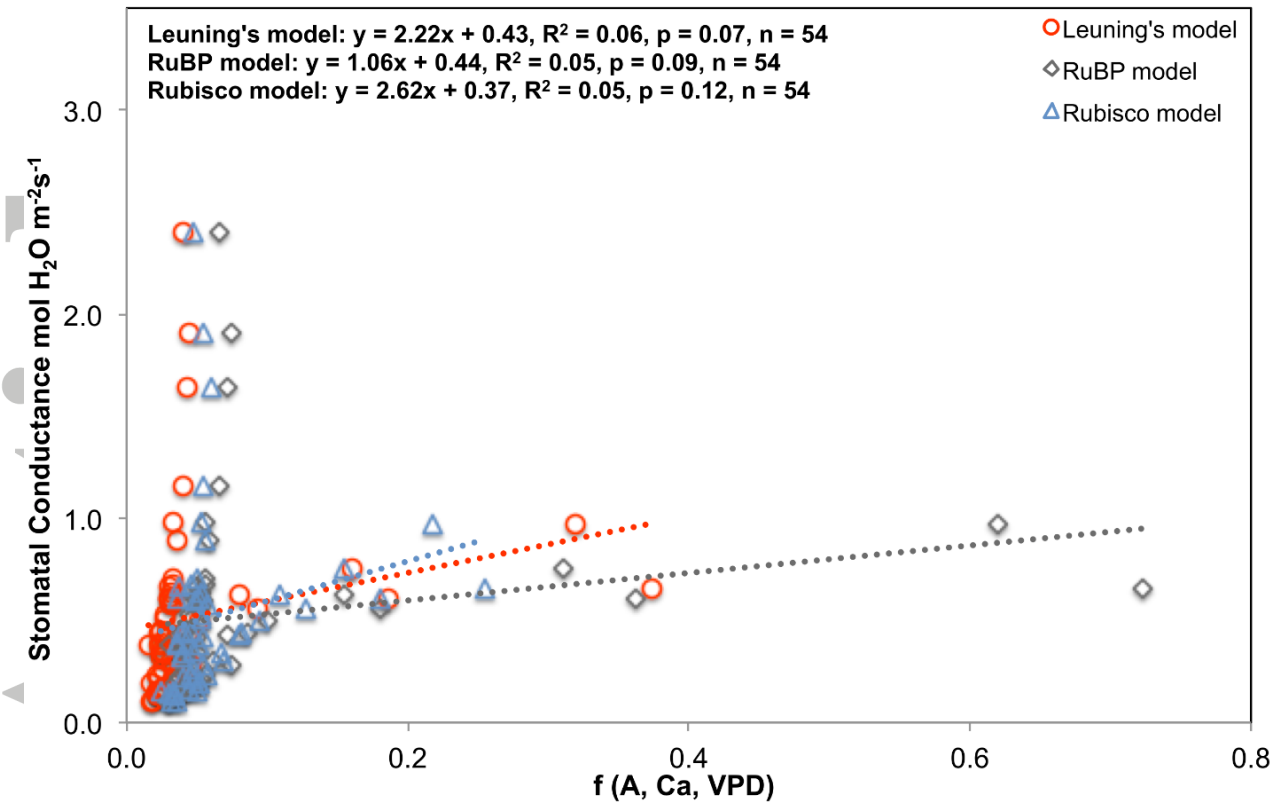
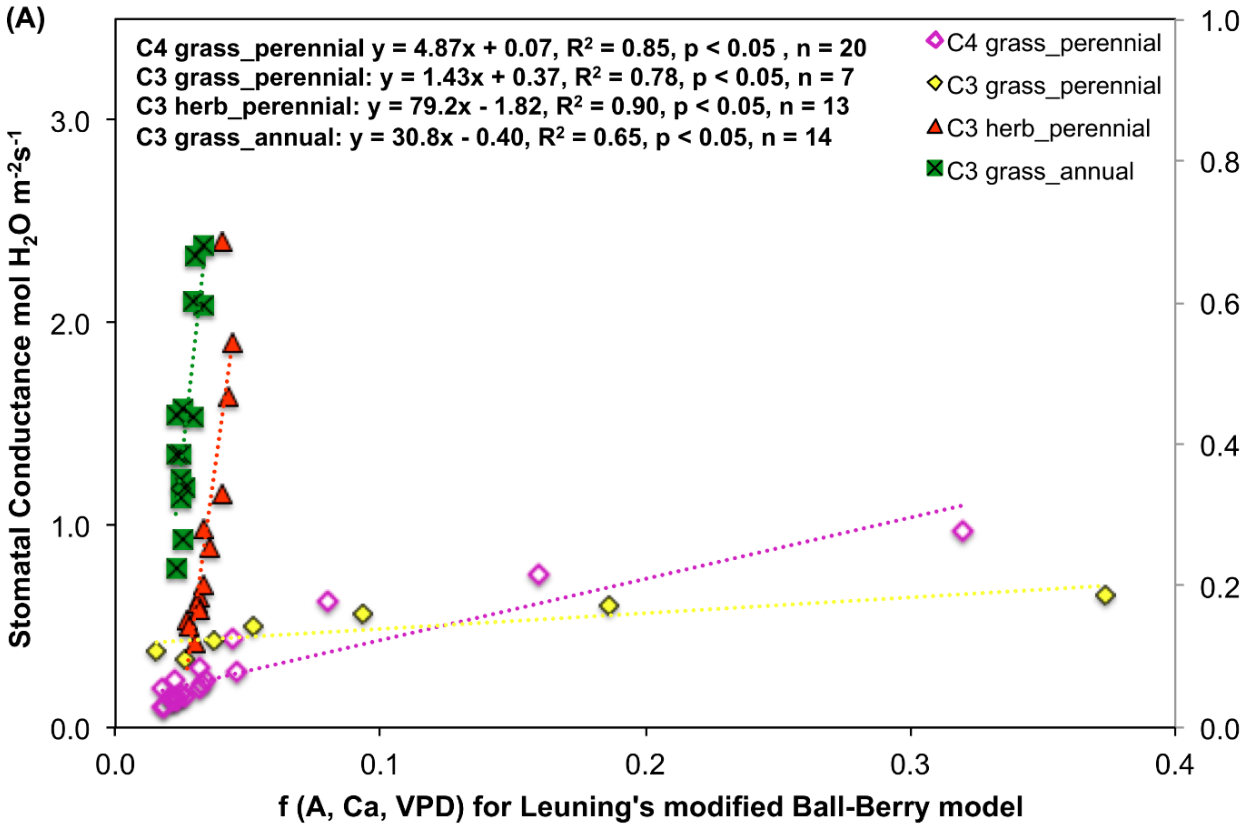
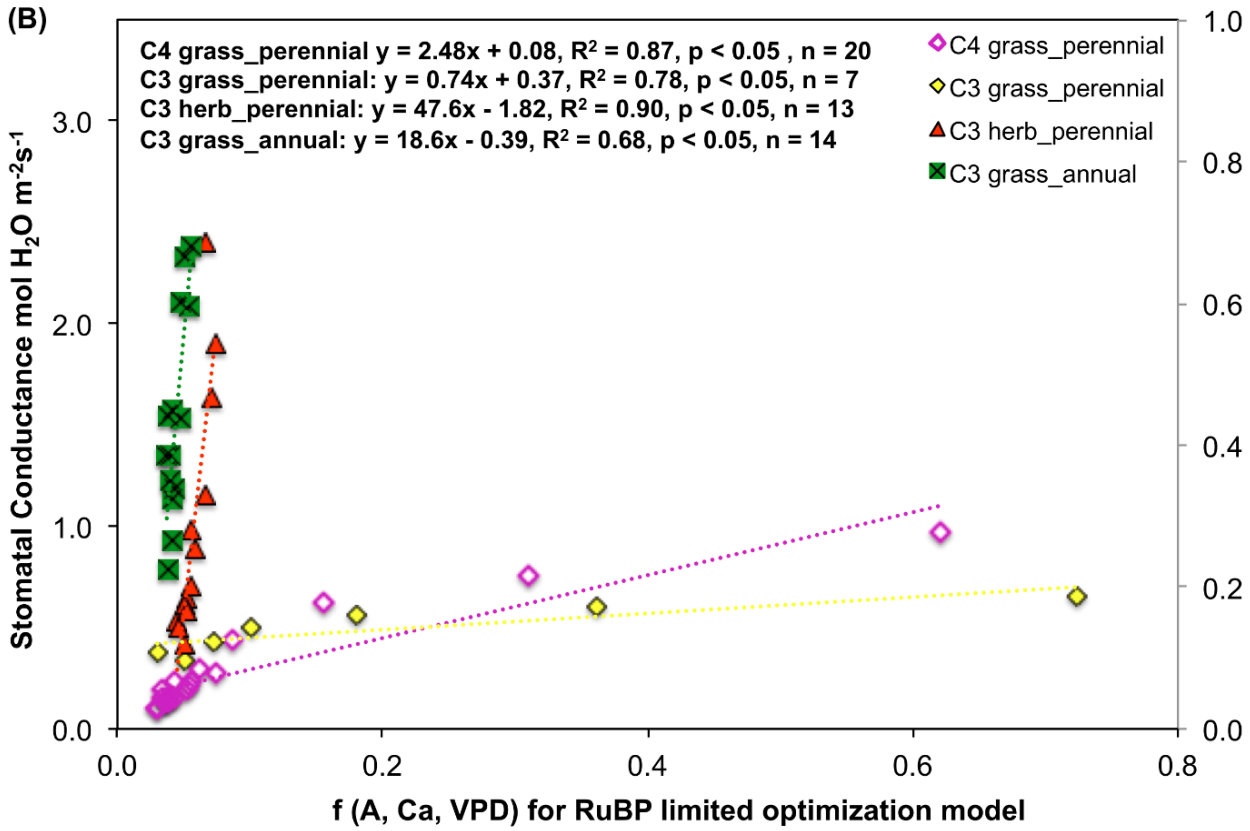


Figure 8. Regression of stomatal conductance g_s as a function of C_a, A, and D for the Leuning's modified Ball-Berry model (red open circles), RuBP limited optimization model (grey open squares), and Rubisco limited optimization model (blue open triangles). The data are from semi-controlled measurements in drylands.





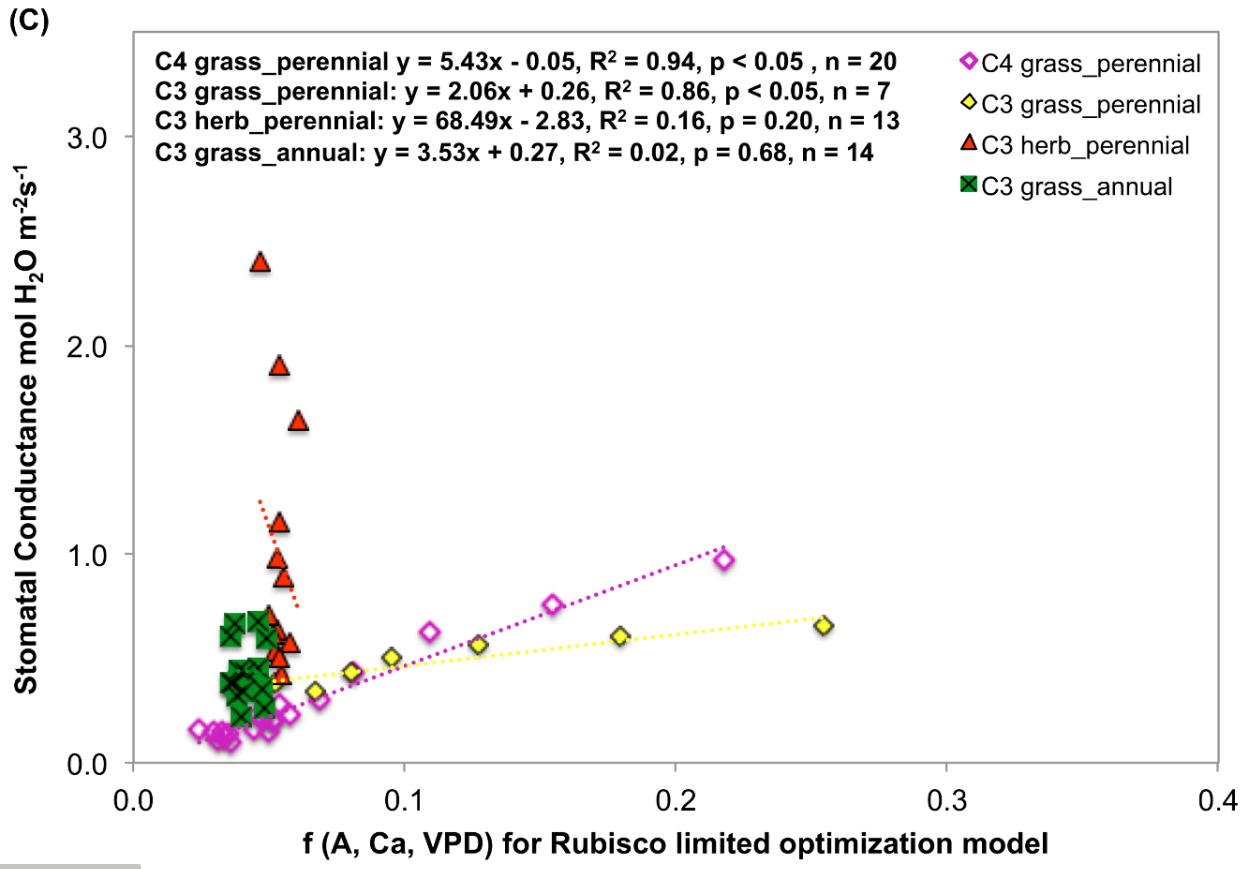


Figure 9. The responses of stomatal conductance g_s as a function of C_a, A, and D for different species and life form, for Leuning's modified Ball-Berry model (A), RuBP limited optimization model (B), and Rubisco limited optimization model (C). The data are from semi-controlled measurements in drylands.